Physiological Response of *Vitis vinifera* L. (cv. Chenin blanc) Grafted onto Different Rootstocks on a Relatively Saline Soil

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Certain physiological parameters, namely leaf water potential, stomatal resistance and rate of photosynthesis of Chenin blanc grafted onto 10 rootstock cultivars on a relatively saline soil under irrigation in a hot region (V), were measured for two growing seasons. Soil electrical resistance, which varied from 632 to 271 ohms in the shallower soil layers (<500 mm) and from 414 to 167 ohms deeper in the soil, decreased during the growing seasons. Although diurnal and seasonal patterns of change of the physiological parameters measured did not differ between rootstock cultivars, significant differences in their magnitudes were apparent. The rootstocks US 16-13-23, 13-5 E.V.E. Jerex were more stressed than 101-14 Mgt, 143-B Mgt and 110 Richter and had lower rates of photosynthesis. Photosynthetic rate was predominantly inversely correlated with stomatal closure. The use of 101-14 Mgt and 143-B Mgt is recommended under relatively saline conditions.

In lower rainfall regions, where leaching of soluble salts is often incomplete, soil salinity can be a serious constraint to agricultural production. Under these conditions inter- and intraspecific variation in salt tolerance can be utilised to enhance crop yield, provided that cultivation practices to prevent salt accumulation in the soil are not neglected.

The presence of excess salts in the soil leads to a decrease in soil osmotic potential and consequently a decrease in its water potential (Salisbury & Ross, 1978). Salinity, therefore, affects plant growth by diminishing the availability of soil water for the plant and increasing the presence of toxic ions (Bernstein, 1975; Gale, 1975; Greenway & Munns, 1980).

Photosynthesis in the grapevine is affected by a number of climatic factors (Smart, 1974; Kriedemann, 1977; Sepulveda & Kliewer, 1986) and cultivation practices (Hofäcker, 1978; Hunter & Visser, 1988; Archer & Strauss, 1990) and is reduced by salinity (Downton, 1977; Walker *et al,* 1981; Downton & Millhouse, 1985). In the grapevine, however, variation in salt tolerance is well known with respect to both the rootstock (Sauer, 1968; Downton, 1985; Arbabzadeh & Dutt, 1987) and scion cultivar (Alexander & Woodham, 1968; Groot Obbink & Alexander, 1973; Barlass & Skene, 1981; West & Taylor, 1984). In a previous study Southey and Jooste (1991) found significant differences in the performance of different graft combinations in a soil of varying salinity. The upper soil layers (<600 mm) of this trial were of a high potential for viticulture but could be prone to salinization (Southey, 1992).

The aim of this investigation was, therefore, a comparative study in order to ascertain the effects of the rootstock/scion combination on certain physiological parameters which may account for differences in grapevine performance on a relatively saline soil.

MATERIALS AND METHODS

Soil analyses: Details of the physical and chemical properties of the vineyard soil were given in previous publications (Southey & Jooste, 1991; Southey, 1992).

At various times during the tenth and eleventh growing seasons the soil was sampled at depths of 0-250 mm, 250-500 mm, 500-750 mm and 750-1000 mm and the electrical resistance and soil water were measured. Soil water was determined gravimetrically while soil electrical resistance of the saturated paste was determined using a standard USDA cup.

Climatic data: Meteorological data were obtained from a standard weather station situated approximately one kilometre from the experimental vineyard. Relative humidity and photosynthetically active radiation were measured

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every two hours in the experimental vineyard using an aspirated psychrometer and LI-1800 portable spectroradiometer (LI-COR Inc, Nebraska, USA), respectively.

Physiological parameters: Physiological measurements commenced with the determination of pre-dawn leaf water potentials at 04:00 and thereafter at two-hourly intervals until 18:00 using the pressure chamber technique (Scholander *et al.*, 1965). The measurement of leaf temperature, photon flux density, stomatal resistance and rate of photosynthesis commenced at 06:00 using a portable infra-red gas analyser (Analytical Development Company) connected in the "open system" of photosynthesis measurement, with an air flow rate of 300 ml/min.

Daily variation of the abovementioned physiological parameters was measured at four developmental stages, namely berry set, pea-size, vèraison and ripeness during the 1989/90 growing season, while the same parameters were measured at ripeness and during drying cycles between irrigations in the following season.

Fully mature leaves, which were situated on the apical third of bearing shoots and exposed to full sunlight, of two visually selected vines of each graft combination were used for all measurements. Measurements were also carried out on leaves in the same position but located in full shade.

Experimental vineyard: The studies were conducted in a ten-year-old *Vitis vinifera* L. cv. Chenin blanc vineyard. The scion was grafted onto ten rootstock cultivars (Table 1). Details of the experimental vineyard and cultivation techniques are given in previous studies (Southey & Jooste, 1991; Southey, 1992).

TABLE 1
Genetic origin and clone numbers of the rootstock cultivars studied in the experimental vineyard at Robertson.

Rootstock Cultivar	Clone	Genetic Origin
13-5 E.V.E. Jerex	66-03-08	*Vitis Berlandieri* Planch.
101-14 Millardet et de Grasset	AA 25	*V. rupestris* Sch. x *V. riparia* Mich.
1045 Paulsen	PZ 1	*V Berlandieri* x Aramon Rupestris Ganzin No. 2 (*V. vinifera* L. x *V. rupestris*).
Ramsey	SC 18	*V. Champini* Planch.
143-B Millardet et de Grasset	BA 32	*V. vinifera* x *V. riparia.*
99 Richter	RY 13	*V. Berlandieri* x *V. rupestris.*
110 Richter	RQ 28	*V. Berlandieri* x *V. rupestris.*
140 Ruggeri	RU 354	*V. Berlandieri* x *V. rupestris.*
US 2-1	-	Jacquez (*V. aestivalis* x *V. cinerea* x *V. vinifera*) x 99 Richter.
US 16-13-23	-	1202 C. (*V. vinifera* x *V. rupestris*) x 99 Richter.

During the tenth growing season the vineyard was irrigated as indicated in Figure 1, with an additional irrigation of 50 mm after harvesting. In the following season the vineyard received four 50 mm irrigations with fresh water from mid-November until after harvesting. The vineyard was fertilised with 170 kg/ha superphosphate (11,3%P) once a year and 150 kg/ha limestone ammonium nitrate (28%N) in two annual instalments of 50 and 100 kg respectively.

Statistical analyses: The statistical software package Genstat (Lawes Agricultural Trust, Rothamsted Experimental Station, United Kingdom) was used to test for significant differences between means.

RESULTS AND DISCUSSION

Soil characteristics: The patterns of depletion of soil water were similar for both the 1989/90 and 1990/91 growing seasons and thus only the data for the 1989/90 growing season are presented in Fig. 1.

As the season progressed the percentage of soil water throughout the soil profiles generally declined as soil water reserves were depleted. Subsequent irrigations did not raise the percentage of soil water to those levels found early in the season (Fig. 1). During each drying cycle soil water was depleted at a faster rate closer to the surface (<500 mm), where the majority of the roots were located (Southey, 1992), than in the deeper soil layers (Fig. 1).

The electrical resistance of the soil to a depth of 500 mm ranged from 632 to 271 ohms (±0,089 to 0,134% NaCl in saturation extract), while deeper in the soil profile (>500 mm) it varied from 414 to 167 ohms (±0,095 to 0,290% NaCl in saturation extract).

Throughout the profile electrical resistance decreased with decreasing soil water, and during both seasons changes in soil electrical resistance followed a similar trend to that found with soil water (Fig. 2). Throughout both growing seasons electrical resistance was highest closest to the surface and decreased with depth. In the upper layers of the soil profile (<500 mm) the electrical resistance increased rapidly after each irrigation with fresh water and then decreased as the soil dried out. In the deeper layers, however, soil electrical resistance showed less variation and was lower even though the percentage of soil water was higher. These results suggest that excess salts were leached from the shallower layers in the profile; this is characteristic of saline soils found in semi-arid regions (Richards *et al.*, 1954).

Climatic conditions: Details of mean daily temperature, relative humidity, evaporation rate and photosynthetically active radiation (PAR) are given in Table 2. It is evident that climatic conditions on each measurement day during the 1989/90 growing season were comparable, with the exception of PAR at berry set and evaporation rate at berry set and pea size. At berry set the mean PAR measured was significantly lower than at the other developmental stages. The hourly variation of PAR is given in Fig. 3. At berry set the PAR was at all times lower than that measured at other developmental stages, with the exception of early in the morning and in the evening.

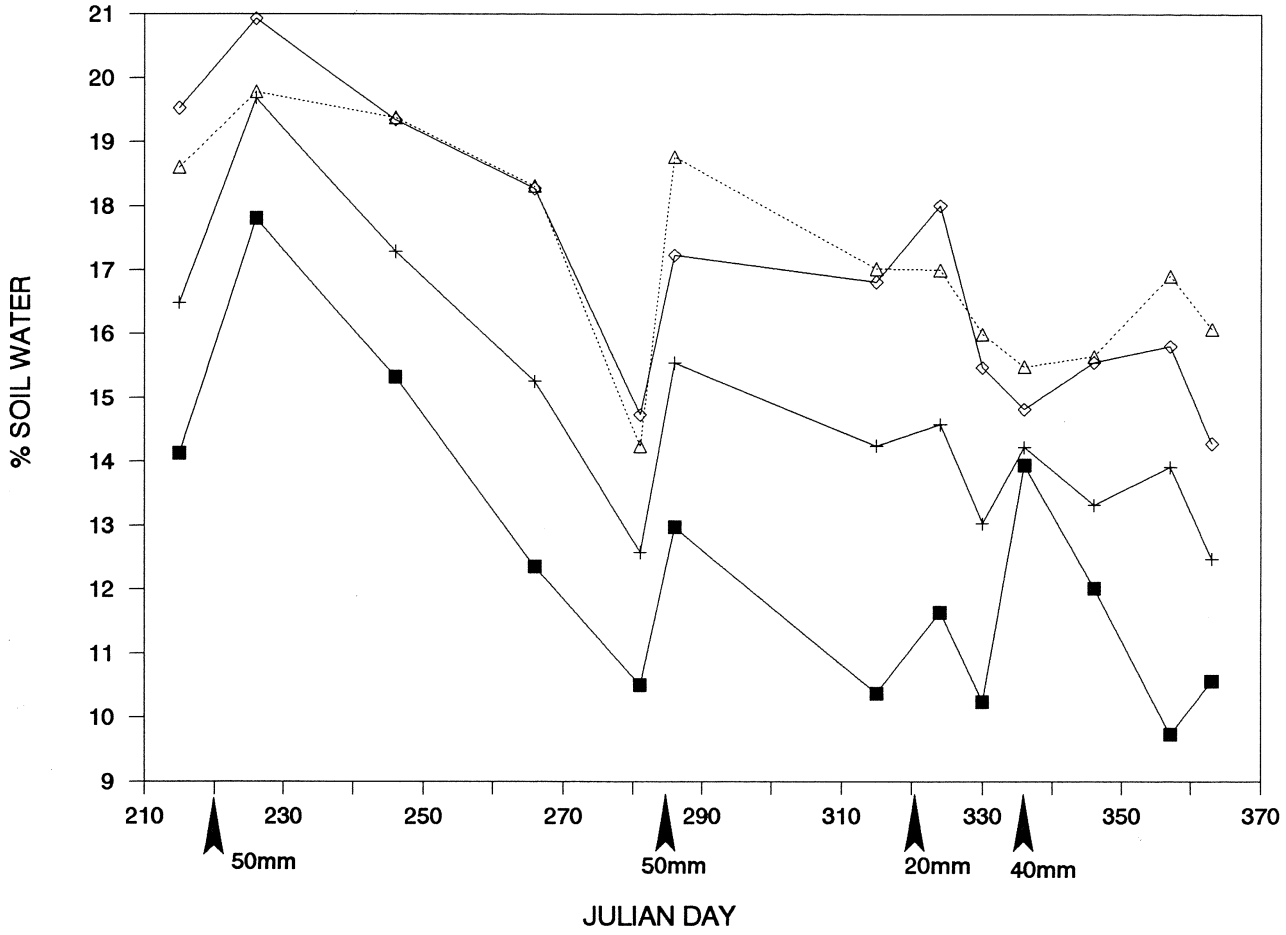

FIGURE 1
Soil water at different depths in the experimental vineyard at Robertson during the 1989/90 growing season. ■ = 0-250 mm, + = 250-500 mm, Δ = 500-750 mm, ◇ = 750-1000 mm. Julian Day 01 = 01-03-89. ▲ denotes irrigation.

Leaf water potentials: On all measurement days the leaf water potentials (LWP) of all graft combinations followed similar daily cycles of change; those of selected rootstocks on a typical measurement day are presented in Fig. 4. The LWPs of sunlit leaves declined rapidly after dawn, when the least negative values were recorded, until a minimum was reached between 12:00 and 14:00. Thereafter LWP increased gradually until dusk (Fig. 4). These daily fluctuations in LWP are typical of those found in the grapevine by other workers (During & Loveys, 1982; Smart & Coombe, 1983; Van Zyl, 1984; Archer & Strauss, 1990) and reflect changes in radiation and atmospheric conditions more than soil water status (Smart & Coombe, 1983).

TABLE 2
Daily means of climatic parameters measured at different developmental stages at Robertson during the 1989/90 growing season.

Developmental Stage	Ambient Temperature (°C)	Relative Humidity (%)	Evaporation Rate (mm day^{-1})	PAR[1] (μmol m^{-2} s^{-1})
Berry Set	32,9	47,7	9,5	1029
Pea size	28,0	48,1	8,5	1169
Vèraison	32,3	48,4	11,0	1130
Ripeness	32,9	48,1	11,0	1149
D (p≤0,05)	-	-	-	77

1. Photosynthetically active radiation.

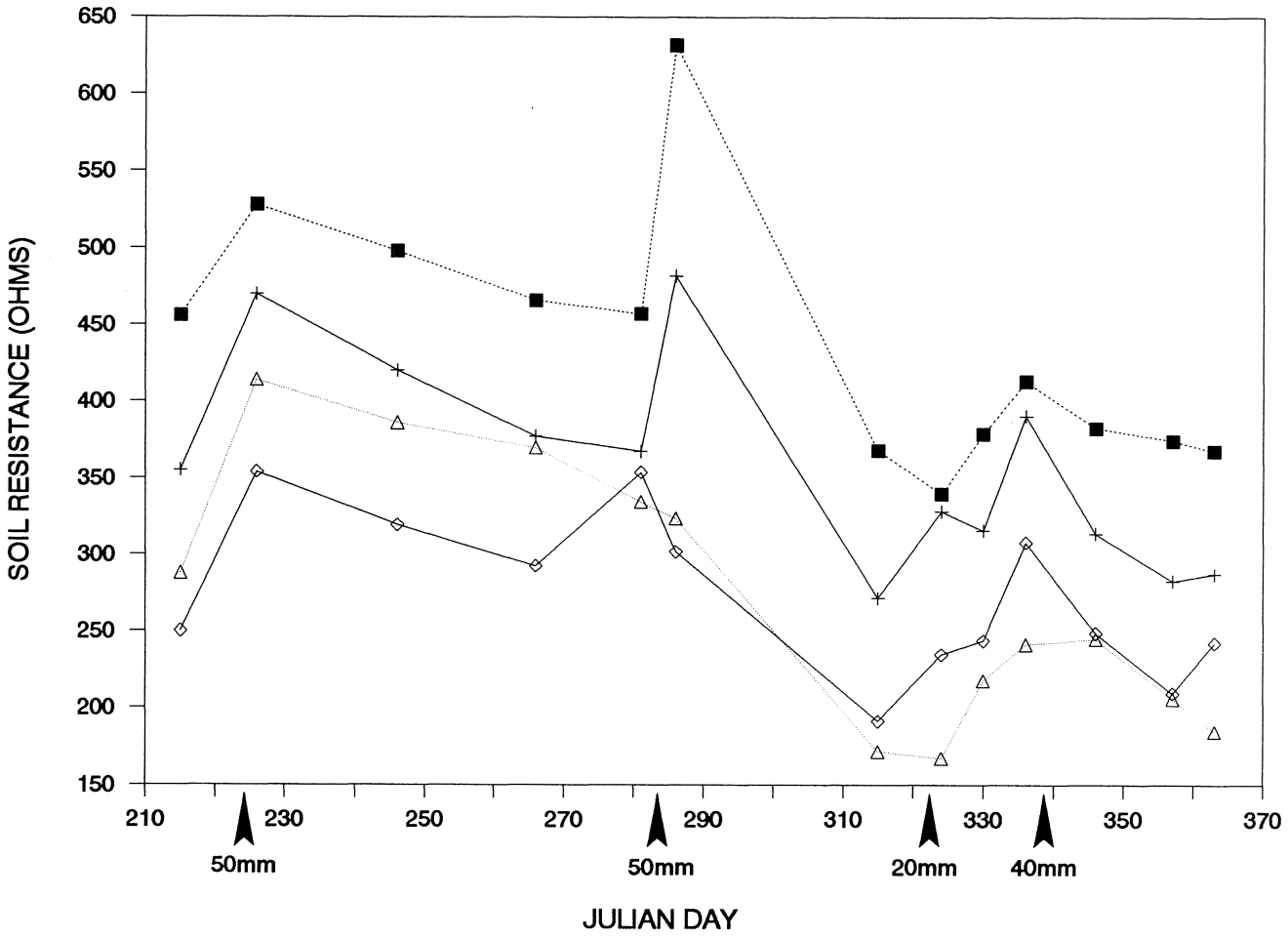

FIGURE 2

Soil electrical resistance at different depths in the experimental vineyard at Robertson during the 1989/90 growing season. ■ = 0-250 mm, + = 250-500 mm, Δ = 500-750 mm, ◇ = 750-1000 mm. Julian Day 01 = 01-03-89. ▲ denotes irrigation.

If the mean daily LWPs of the rootstocks relative to the mean of all rootstocks at all developmental stages (which is given an arbitrary value of zero) are used as an indication of the extent of water stress, then rootstock and seasonal effects are clearly discernable (Fig. 5). The rootstocks US 16-13-23, US 2-1, 99 Richter and 13-5 E.V.E. Jerex were relatively more stressed than 140 Ruggeri, 1045 Paulsen, 143-B Mgt and 101-14 Mgt.

All graft combinations became progressively more stressed as the season advanced, until maximum values were attained at vèraison and ripeness (Fig. 5). Since LWP was found to be highly correlated to climatic factors such as ambient radiation, temperature and relative humidity (During & Loveys, 1982; Smart & Coombe, 1983; Van Zyl, 1984), seasonal changes in LWP could be the consequence of changes in climatic factors.

Pre-dawn leaf water potentials (LWP_d), on the other hand, are more closely associated with the water potential of the soil (Smart & Coombe, 1983; Van Zyl, 1984; Nagarajah, 1989) and were also found to decrease as the season progressed (Table 3a). These more closely reflected changes in soil water and electrical resistance of the soil, particularly of the upper soil layers (Figs. 1 & 2), where the majority of the roots were located (Southey, 1992).

Although not apparent at all developmental stages, the LWP_ds of US 16-13-23, 99 Richter and US 2-1 were significantly lower over the season than those of 110 Richter, 143-B Mgt, Ramsey and 140 Ruggeri (Table 3a).

In an earlier study (Southey, 1992) US 16-13-23 was found to have a relatively low root density (root number m^{-2}); this could have resulted in poorer water uptake and consequently more negative LWP_ds. Furthermore, US 16-13-23 had a higher percentage of its roots in the deeper, more saline soil layers (> 500 mm).

Ramsey, which was less stressed than US 16-13-23 [significantly less negative LWP_d (Table 3a)], had a lower root density than the latter rootstock (Southey, 1992) and thus considering the above, one would anticipate a lower LWP_d. The greater percentage of its roots, however, were located closer to the soil surface (<500 mm), where soil electrical resistances were higher. Conversely, 13-5 E.V.E. Jerex, which was significantly more stressed (Table 3a), had a relatively high root density but a higher percentage of its roots were in the deeper, more saline layers (Southey, 1992). These results suggest that in this soil the extent of stress of the different rootstocks, as indicated by LWP_d, was closely associated to both root density and root distribution.

Similarly, minimum leaf water potentials (LWP_m), measured at 12:00, also decreased as the season progressed but did not differ significantly between the rootstocks at all developmental stages (Table 3b). These results suggest that diurnal changes in climatic conditions did not affect all the rootstocks to the same extent.

Using LWP_d as an indication of water stress, the study showed that US 16-13-23 was more stressed than all the other rootstocks during the 1989/90 season, with the exception of 99 Richter (Table 3a). This was also apparent during the following growth season (data not shown).

Stomatal resistance: Although the magnitude of stomatal resistance of sunlit leaves varied between individual rootstock cultivars and developmental stages, the daily cycles of change were generally similar for all rootstocks at all developmental stages in both seasons. These daily changes in stomatal resistance of sunlit leaves of selected rootstocks on a typical measurement day are presented in Fig. 6. Stomatal resistance decreased rapidly from 06:00 until a minimum was reached between 08:00 and 10:00. Thereafter, stomatal resistance increased with maxima being recorded between 12:00 and 14:00 and at 18:00. These results are in accordance with those of other researchers (During & Loveys, 1982; Smart & Coombe, 1983; Van Zyl, 1984; Archer & Strauss, 1990).

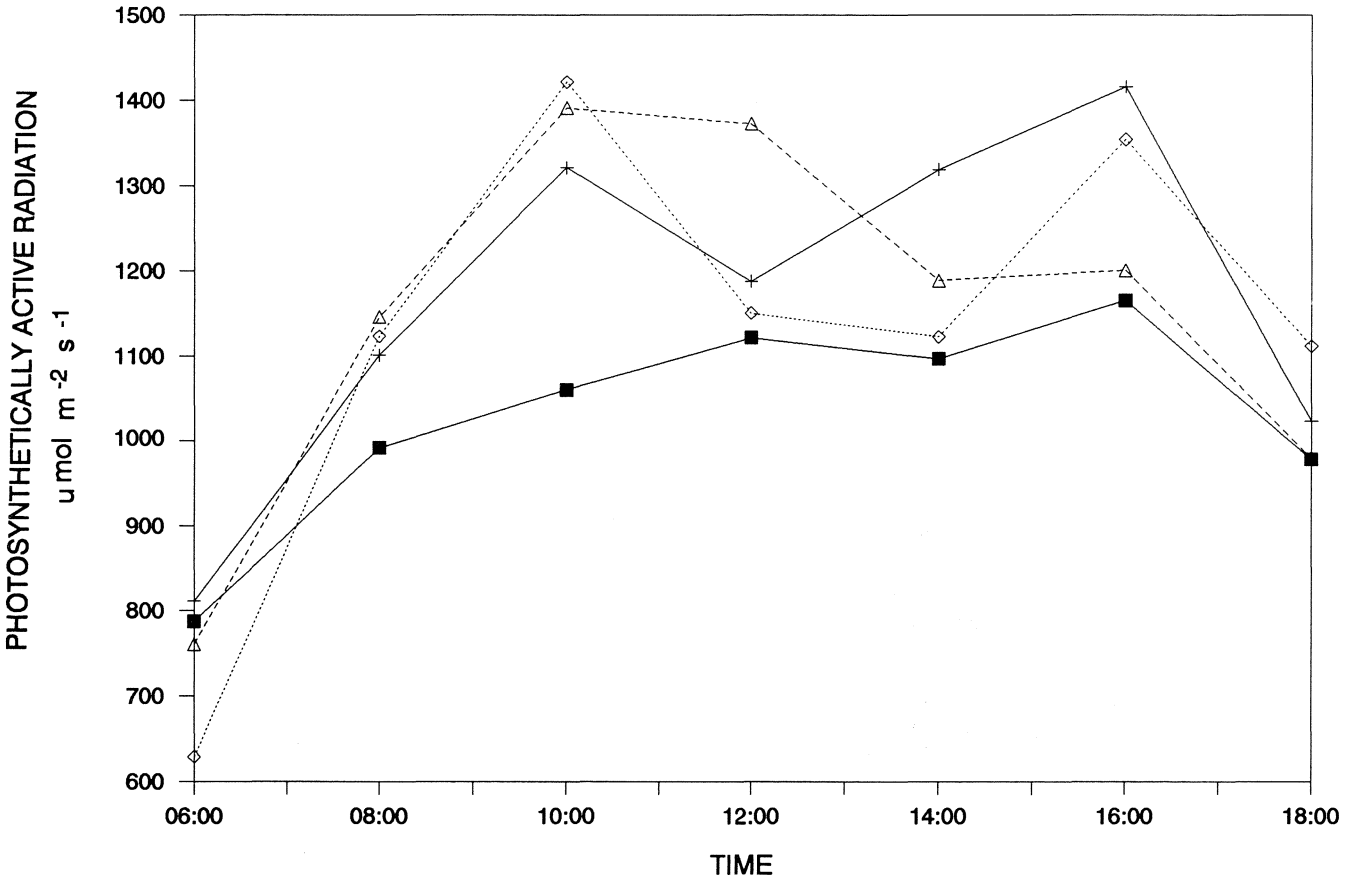

FIGURE 3
Diurnal variation in photosynthetically active radiation (μmol m^{-2} s^{-1}) measured in the experimental vineyard at Robertson at different developmental stages during the 1989/90 growing season. ■ = Berry set, + = Pea size, Δ =Vèraison, ◇ = Ripeness.

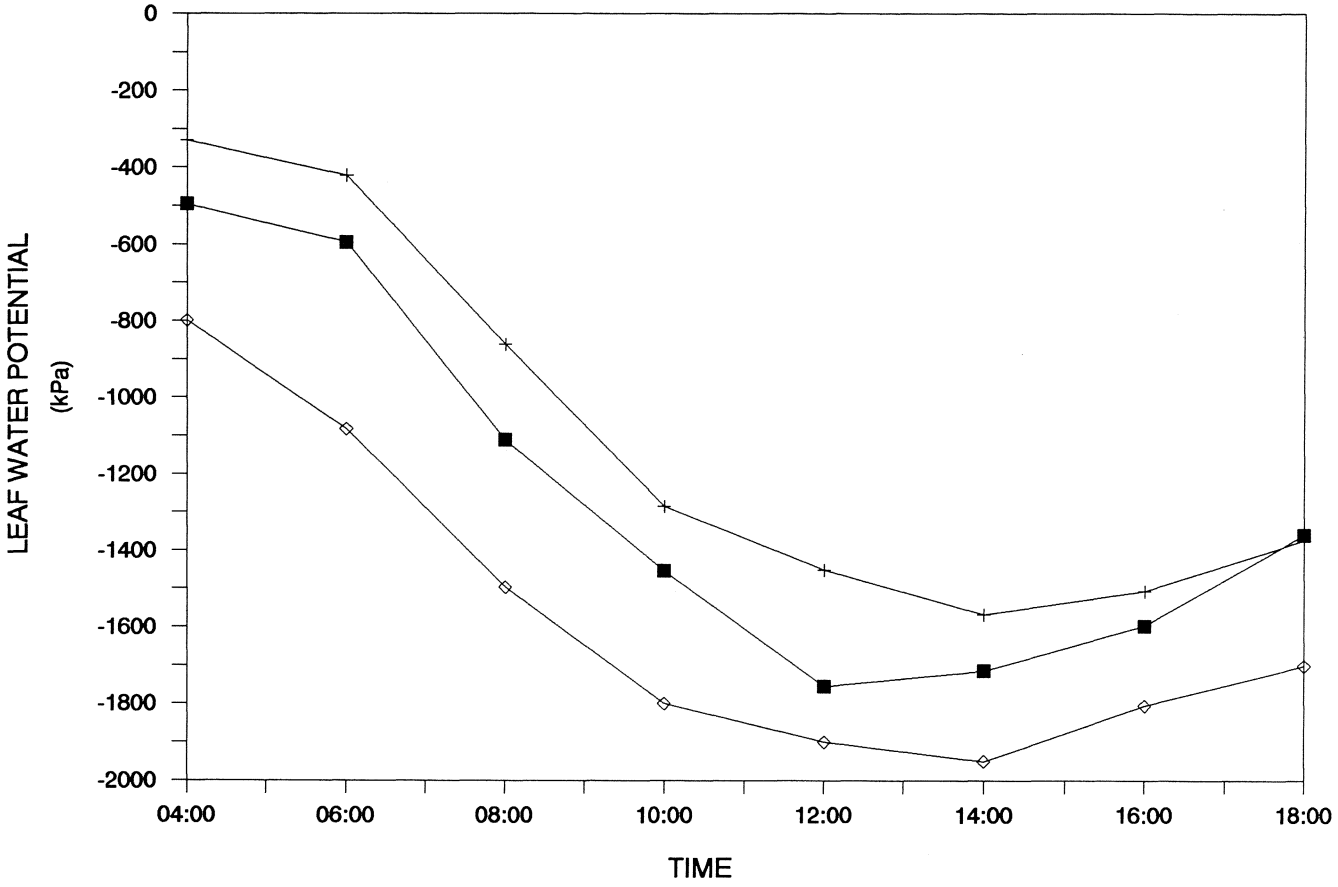

FIGURE 4

Diurnal variation in leaf water potential (kPa) of selected rootstocks at vèraison in a relatively saline soil. ■ = Mean, ◇ = US 16-13-13, + = 110 Richter.

TABLE 3a

Leaf water potentials (kPa) at different developmental stages of Chenin blanc grafted onto different rootstock cultivars in a relatively saline soil during the 1989/90 growing season at Robertson. Pre-dawn leaf water potentials (measured at 04:00).

Rootstock Cultivar	Developmental Stage				Mean
	Berry Set	Pea Size	Vèraison	Ripeness	
US 16-13-23	-483	-526	-799	-828	-659
99 Richter	-367	-475	-659	-770	-568
US 2-1	-388	-515	-578	-731	-553
101-14 Mgt	-319	-432	-516	-809	-519
13-5 E.V.E. Jerex	-245	-514	-578	-684	-505
1045 Paulsen	-220	-463	-446	-726	-464
140 Ruggeri	-221	-471	-329	-780	-450
Ramsey	-331	-366	-303	-768	-442
143-B Mgt	-194	-382	-380	-809	-441
110 Richter	-270	-358	-372	-670	-418
Mean	-304	-450	-496	-758	-502
D (p≤0,05)	161	196	233	257	99

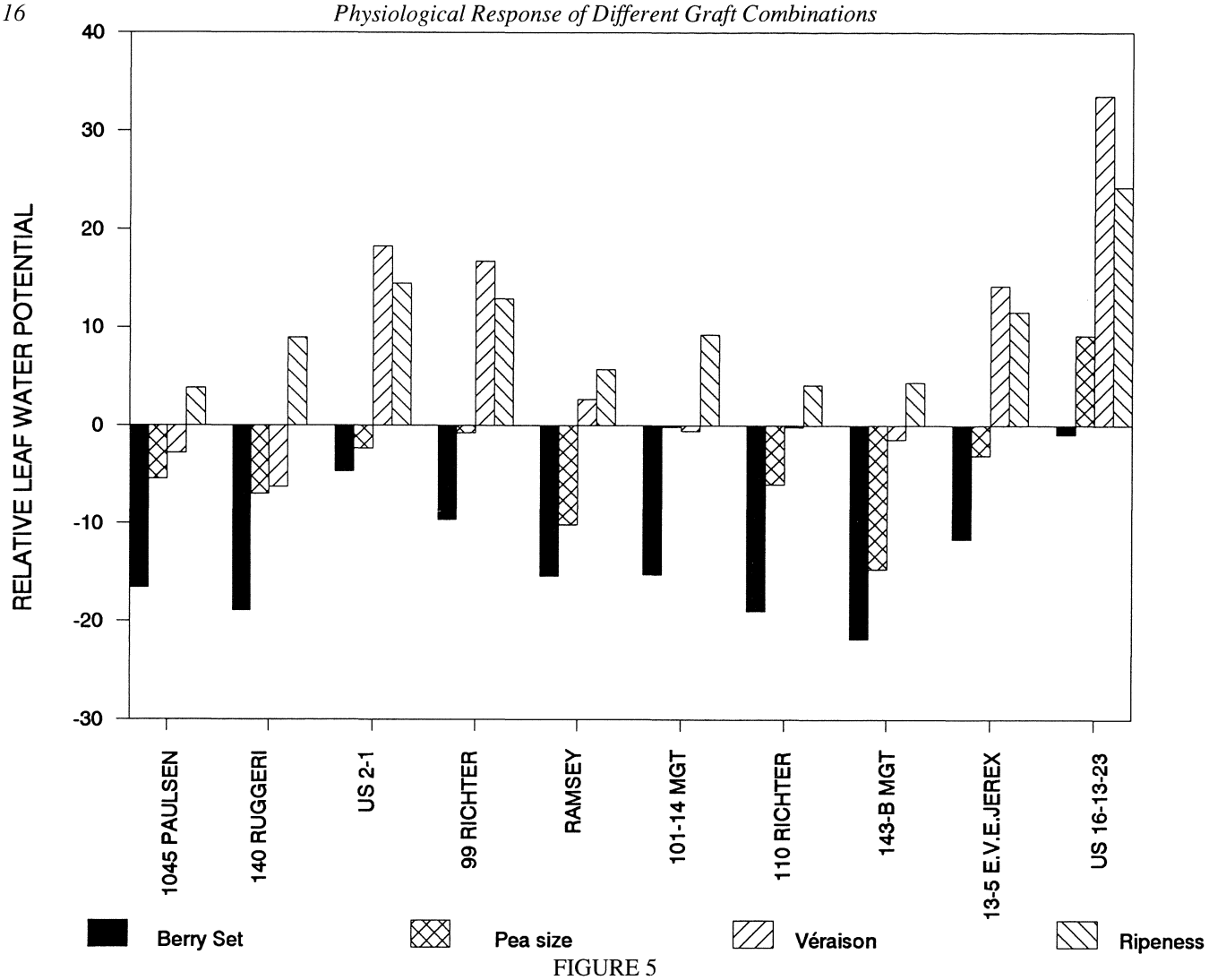

FIGURE 5

Relative leaf water potential (relative to the mean of all rootstocks at all developmental stages) of Chenin blanc grafted onto different rootstock cultivars in a relatively saline soil at different developmental stages during the 1989/90 growing season at Robertson. A higher positive relative leaf water potential indicates a more negative actual leaf water potential.

TABLE 3b

Leaf water potentials (kPa) at different developmental stages of Chenin blanc grafted onto different rootstock cultivars in a relatively saline soil during the 1989/90 growing season at Robertson. Minimum leaf water potentails (measured at 12:00).

Rootstock Cultivar	Developmental Stage				Mean
	Berry Set	Pea Size	Vèraison	Ripeness	
US 2-1	-1631	-1636	-1897	-1880	-1761
US 16-13-23	-1613	-1631	-1900	-1848	-1748
13-5 E.V.E. Jerex	-1415	-1670	-1859	-1893	-1709
101-14 Mgt	-1574	-1663	-1692	-1711	-1660
110 Richter	-1366	-1533	-1749	-1974	-1656
99 Richter	-1525	-1560	-1834	-1672	-1648
143-B Mgt	-1451	-1451	-1765	-1701	-1592
140 Ruggeri	-1338	-1568	-1452	-1795	-1538
Ramsey	-1319	-1461	-1633	-1672	-1521
1045 Paulsen	-1255	-1404	-1775	-1539	-1493
Mean	-1449	-1558	-1756	-1768	-1633
D (p≤0,05)	433	334	587	288	204

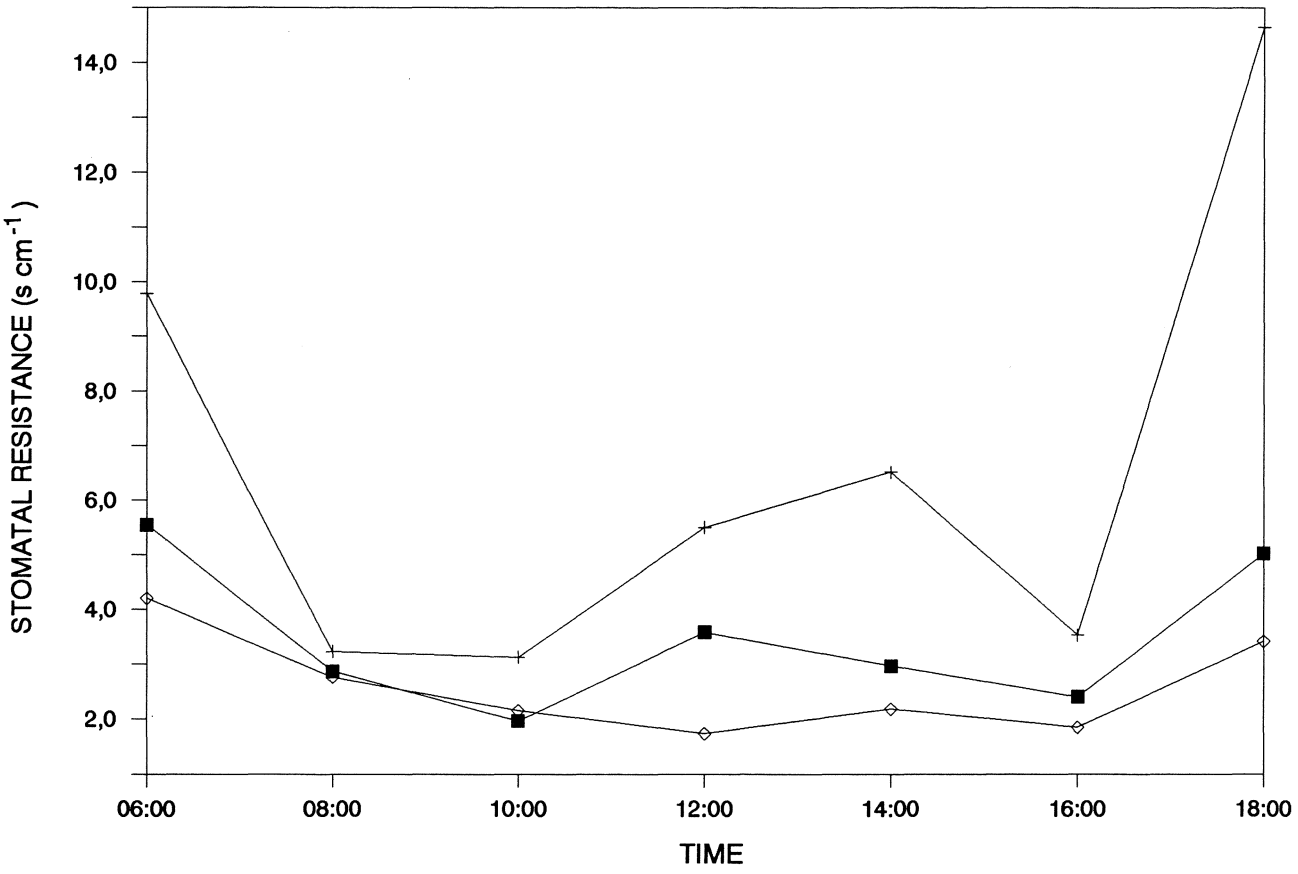

FIGURE 6

Diurnal variation in stomatal resistance (s cm^{-1}) of selected rootstocks at vèraison in a relatively saline soil. ■ = Mean, + = US 16-13-23, ◇ = 140 Ruggeri.

Although environmental effects on stomatal opening are complex, it is significantly affected by light intensity (Smart & Coombe, 1983; Van Zyl 1984): stomatal resistance was higher in the shaded leaves than in the leaves exposed to full sunlight (data not shown). Further, stomatal closure occurs also at low LWPs (Liu *et al.*, 1978; Smart & Coombe, 1983, Nagarajah, 1989). These factors suggest that early in the day, when LWPs are relatively high, stomatal opening occurred with increasing light intensity. Later in the day, however, despite high light intensities, the stomatal closed as a consequence of, amongst other things, the lower LWPs. The similarity in the daily cycles of stomatal resistance of the different rootstocks suggests that these diurnal changes are predominantly a function of the environment.

Stomatal resistances recorded in this trial were highest at berry set and lowest at pea size, whereafter they increased as the season progressed (Table 4). The high resistances found at berry set were possibly the consequence of the lower light intensity measured at that stage (Table 2) or slightly less mature leaves.

The climatic conditions measured at all stages, with the exception of berry set, were comparable (Table 2) and although a progressive seasonal increase in stomatal resistance has also been reported elsewhere (Hunter & Visser, 1988), the possible effect of the seasonal increase in LWP_d cannot be excluded (Table 3a).

Despite similarities in the diurnal and seasonal changes of stomatal resistance between different rootstock cultivars, the magnitude of the resistances measured was significantly affected by the rootstock (Table 4). Over the season, the stomatal resistance of US 16-13-23 was significantly higher than that of all the other rootstocks, while the stomatal resistance of 101-14 Mgt, 110 Richter, 143-B Mgt, 140 Ruggeri and Ramsey was significantly lower than that of 13-5 E.V.E. Jerex, US 2-1 and 99 Richter. In order to isolate rootstock effects, the rootstocks were compared on a relative scale where the mean stomatal resistance of each developmental stage was given an arbitrary value of zero (Fig. 7).

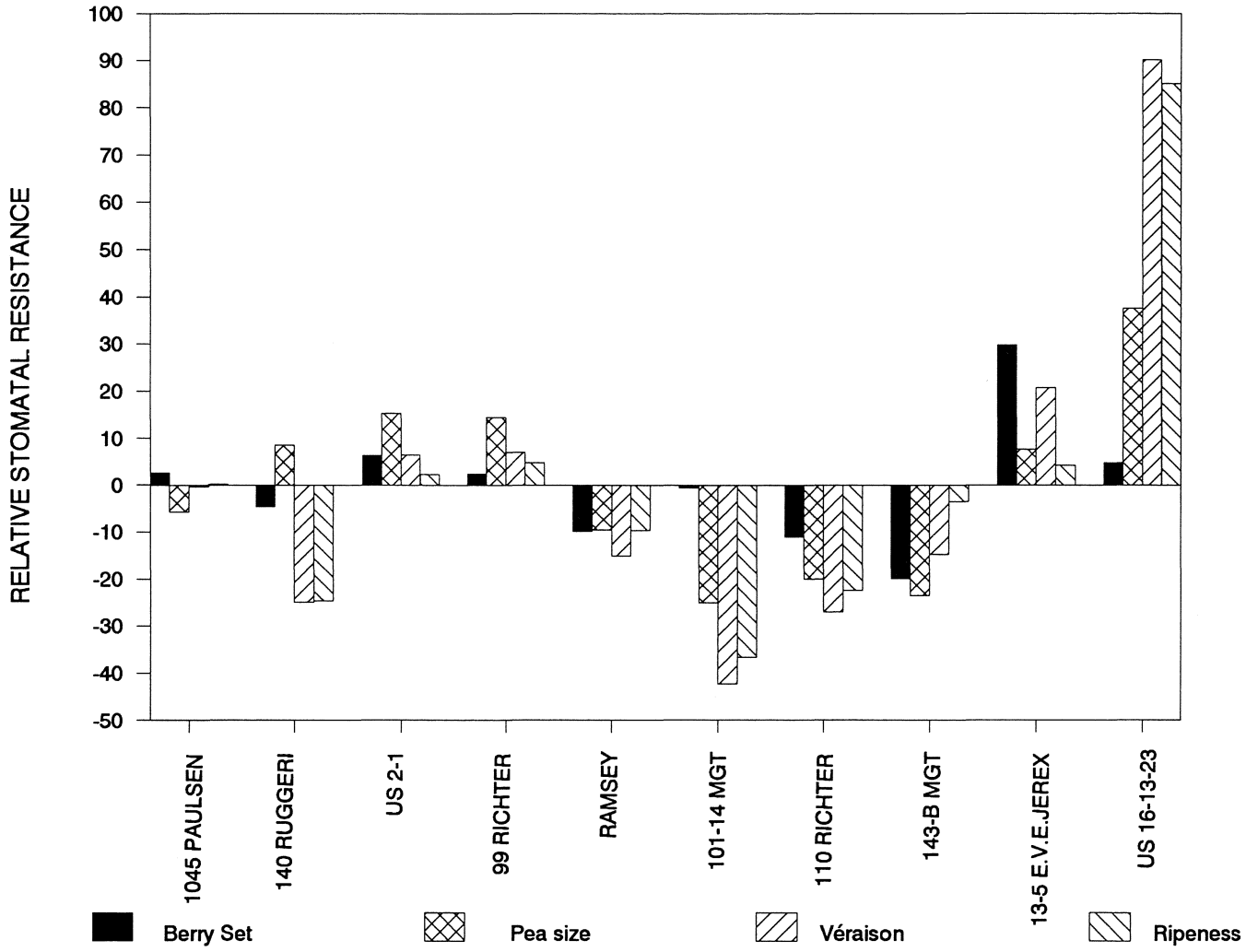

FIGURE 7

Relative stomatal resistance (relative to the mean of all rootstocks at each developmental stage) of Chenin blanc grafted onto different rootstock cultivars in a relatively saline soil at different developmental stages during the 1989/90 growing season at Robertson.

From Fig. 7 it is evident that the relative stomatal resistance of US 16-13-23, 13-5 E.V.E. Jerex, 99 Richter and US 2-1 was higher at all developmental stages than that of 101-14 Mgt, 110 Richter, 143-B Mgt and Ramsey, and seemed to coincide with the LWPs found with these rootstocks.

Rate of photosynthesis: The rates of photosynthesis of Chenin blanc grafted onto different rootstocks were similar for both growing seasons and thus only the data for the 1989/90 season are presented. Mean daily photosynthetic rates ranged from 1,64 μmol $m^{-2}s^{-1}$ to 6,99 μmol $m^{-2}s^{-1}$ (Table 5) and were comparable to those found for other grapevine cultivars by other researchers (Hofäcker, 1978; Hunter & Visser, 1988, Archer & Strauss, 1990).

At all developmental stages diurnal changes in the rate of photosynthesis of all rootstocks followed similar patterns (Fig. 8), reflecting changes in climatic conditions, and were in agreement with those reported elsewhere (Downton, Grant & Loveys, 1987; Archer & Strauss, 1990).

The rates of photosynthesis of different graft combinations differed significantly at all developmental stages (Table 5). The seasonal mean rate of photosynthesis of 110 Richter, 101-14 Mgt, 143-B Mgt and 1045 Paulsen were significantly higher than those found with the other graft combinations. When compared relative to the mean of all rootstocks at all developmental stages, both rootstock and seasonal effects are discernable (Fig. 9). Although not quantified, the leaves of those rootstocks with significantly lower rates of photosynthesis did not have visible symptoms of salt damage. This is in agreement with the finding of Southey (unpublished data) that low levels of salt stress under controlled conditions reduced photosynthetic rates, despite the absence of visible symptoms of salt stress.

At berry set photosynthetic rates were significantly lower than those measured at pea-size, vèraison and ripeness (Table 5). This could have been the consequence of slightly less mature leaves or the lower light intensity measured at this stage (Table 2). Photosynthetic rates of the majority of rootstocks, however, increased up to vèraison, whereafter they decreased. Although the photosynthetic rates of the more basal leaves have been found to decrease during the

growing season (Kriedemann, 1977; Hunter & Visser, 1988), those of the leaves situated closer to the shoot apex tend to increase (Hunter & Visser, 1988). The leaves measured in this trial were of similar age and coincided more with the apical leaves measured by Hunter & Visser (1988).

The rates of photosynthesis of 13-5 E.V.E. Jerex and US 16-13-23 were relatively low throughout the growing season, while their stomatal resistances were relatively high (Fig. 10). Conversely, 101-14 Mgt, 110 Richter and 143-B Mgt had high rates of photosynthesis associated with low stomatal resistances. These results suggest that rates of photosynthesis were a function of the extent of stomatal opening. Ramsey, however, had a relatively low rate of photosynthesis; its stomatal resistance was also low which indicates possible disruption of its photosynthetic apparatus (Fig. 10). Toxic ions, such as chloride, have been found to accumulate in the leaves under saline conditions and to reduce photosynthesis (Downton & Millhouse, 1985). Whether this leads to the low rates of photosynthesis associated with low stomatal resistances is currently being investigated.

TABLE 4

Stomatal resistances (s cm^{-1}) of Chenin blanc grafted onto different rootstocks in a relatively saline soil at different phenological stages during the 1989/90 growing season at Robertson.

Rootstock Cultivar	Developmental Stage				Mean
	Berry Set	Pea Size	Vèraison	Ripeness	
US 16-13-23	6,32	3,14	6,62	6,95	5,76
13-5 E.V.E. Jerex	7,82	2,46	4,21	3,92	4,60
US 2-1	6,41	2,63	3,71	3,84	4,15
99 Richter	6,17	2,61	3,73	3,94	4,11
1045 Paulsen	6,19	2,15	3,47	3,77	3,90
Ramsey	5,44	2,07	2,96	3,40	3,46
140 Ruggeri	5,75	2,48	2,62	2,84	3,42
143-B Mgt	4,83	1,75	2,97	3,63	3,29
110 Richter	5,36	1,83	2,54	2,92	3,16
101-14 Mgt	5,99	1,71	2,01	2,38	3,03
Mean	6,03	2,28	3,48	3,76	3,89
D ($p \leq 0,05$)	1,26	0,40	0,91	0,58	0,47

TABLE 5

Rate of photosynthesis (µmol m^{-2} s^{-1}) of Chenin blanc grafted onto different rootstock cultivars in a relatively saline soil at different developmental stages during the 1989/90 growing season at Robertson.

Rootstock Cultivar	Developmental Stage				Mean
	Berry Set	Pea Size	Vèraison	Ripeness	
110 Richter	2,61	4,90	6,99	5,06	4,89
101-14 Mgt	2,02	4,69	6,95	5,69	4,84
143-B Mgt	2,16	5,36	6,06	5,06	4,66
1045 Paulsen	3,02	5,05	5,45	4,60	4,53
US 2-1	2,74	4,46	4,56	5,24	4,25
99 Richter	2,45	4,09	5,34	4,85	4,18
140 Ruggeri	2,56	3,88	5,31	4,97	4,18
Ramsey	2,39	4,03	4,12	4,63	3,79
13-5 E.V.E. Jerex	1,64	4,94	4,02	4,05	3,66
US 13-16-23	1,75	3,40	3,74	2,21	2,78
Mean	2,33	4,48	5,25	4,64	4,18
D ($p \leq 0,05$)	0,48	0,56	0,51	0,53	0,27

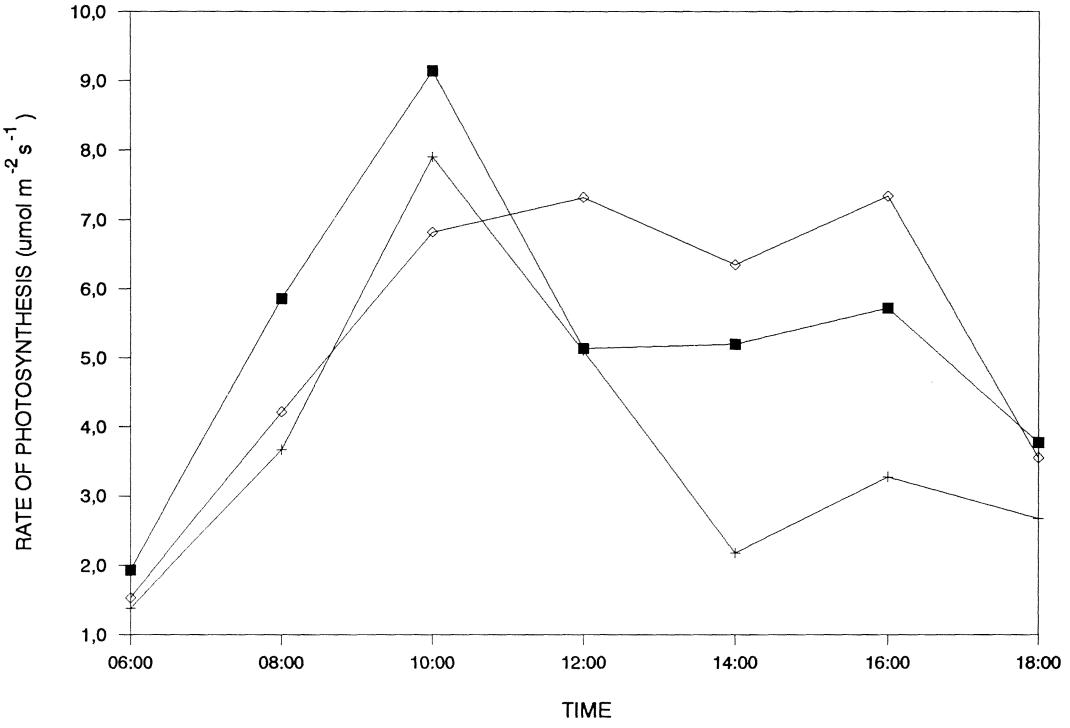

FIGURE 8
Diurnal variation in rates of photosynthesis (µmol $m^{-2}s^{-1}$) of selected rootstocks at vèraison in a relatively saline soil. ■ = Mean, + = US 16-13-23, ◇ = 140 Ruggeri.

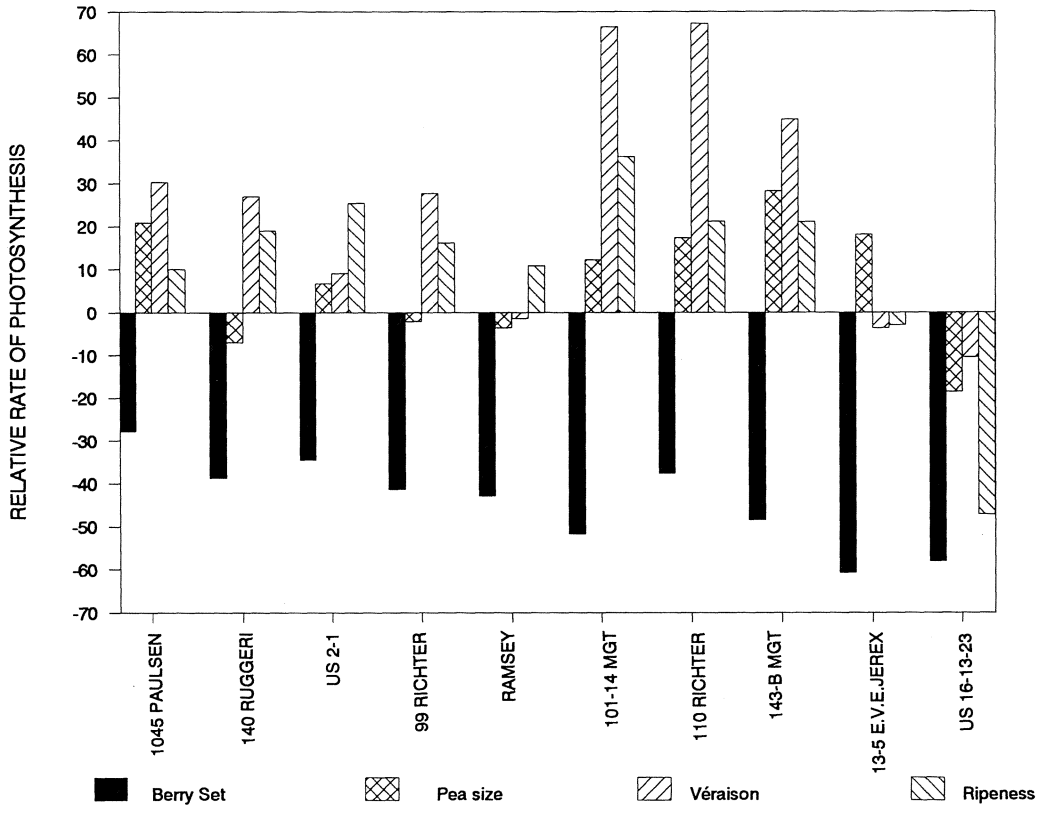

FIGURE 9
Relative rate of photosynthesis (relative to the mean of all rootstocks at all developmental stages) of Chenin blanc grafted onto different rootstock cultivars in a relatively saline soil at different developmental stages during the 1989/90 growing season at Robertson.

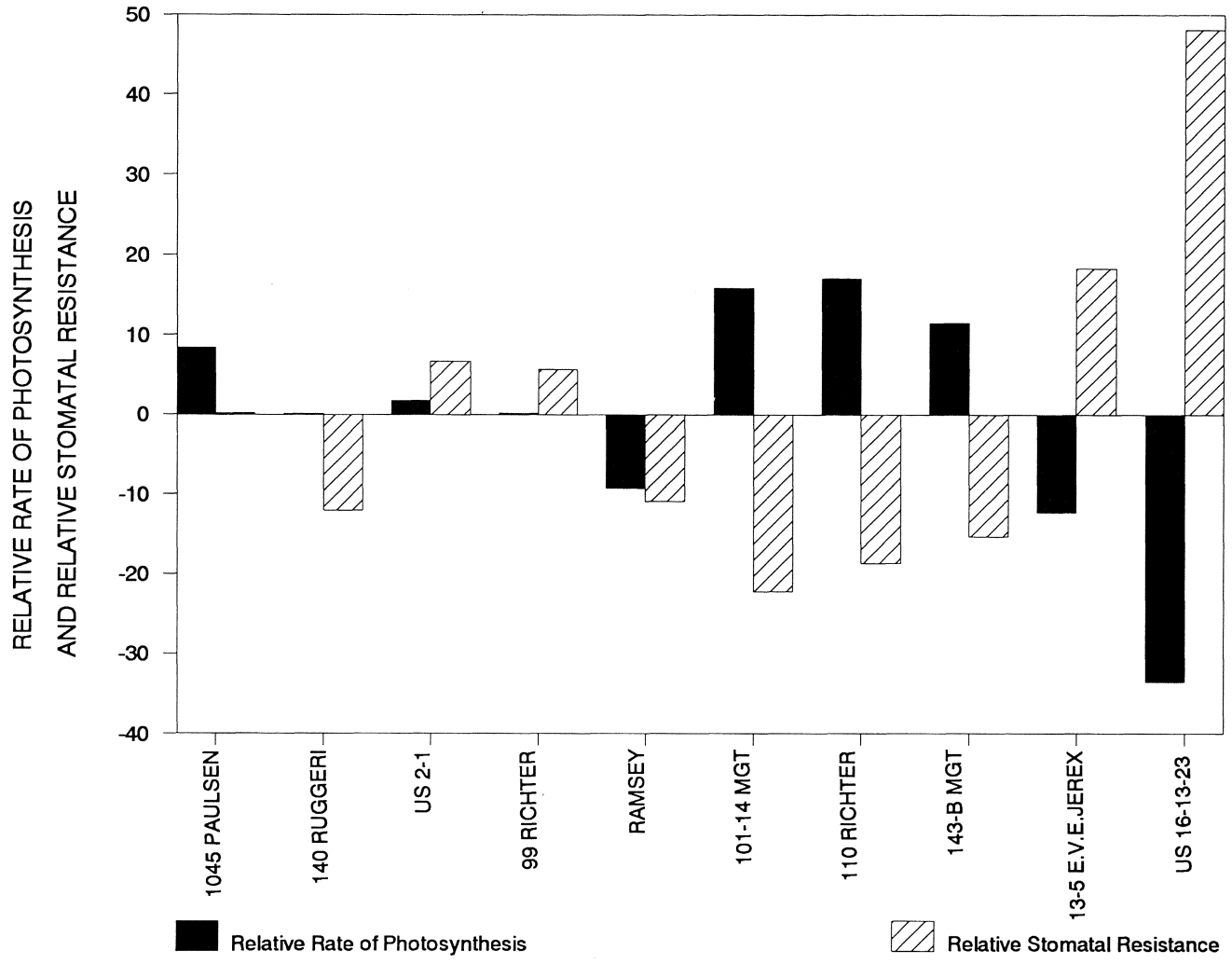

FIGURE 10
Relative rate of phototsynthesis and relative stomatal resistance (relative to the mean of all rootstocks at all developmental stages) of Chenin blanc grafted onto different rootstock cultivars in a relatively saline soil during the 1989/90 growing season at Robertson.

Increasing photosynthetic rates from pea size to vèraison were associated with increasing stomatal resistances, suggesting possible increased photosynthetic efficiency. Hunter & Visser (1988) found increased rates of photosynthesis per unit area with decreasing leaf area caused by defoliation. Although they were not quantified, at the end of the growing season differences in leaf area were observed between the different rootstocks; this could account for differences in photosynthetic efficiency. According to Downton, Grant & Loveys (1987) different crop levels can also lead to differences in stomatal closure by affecting source/sink relationships. In this trial, however, crop levels were consistent with all graft combinations. These aspects require further research.

The results found in this trial suggest that the differences in rates of photosynthesis found between rootstocks were predominantly the result of differences in stomatal closure, which in turn were a result of differences in LWPs.

CONCLUSIONS

The rootstock cultivars studied differed significantly with respect to their physiological response in a soil of varying electrical resistance. The rootstocks US 16-13-23 and 13-5 E.V.E. Jerex were more stressed, as indicated by their higher stomatal resistances and more negative LWPs, than 101-14 Mgt, 143-B Mgt and 110 Richter.

Diurnal variation in LWP, stomatal resistance and rate of photosynthesis was similar for all rootstocks, reflecting changes in climatic conditions. Low electrical resistances in the soil, therefore, did not result in significant changes in diurnal variation.

The relatively low soil water content and low electrical resistances of the soil late in the season resulted in stomatal closure which was associated with reduced rates of photosynthesis. There was evidence of possible compensatory increases in photosynthetic efficiency per unit area, but this aspect requires further research with the quantification of leaf area of the different rootstocks.

The rootstocks 101-14 Mgt and 143-B Mgt appear to be relatively well adapted to saline conditions, as indicated by relatively low levels of stress found in this trial. In a trial in the same location, but with Colombard grafted onto different rootstocks, the performance of these rootstocks was better than that of US 16-13-23 (Southey & Jooste, 1991). The use of 101-14 Mgt and 143-B Mgt can, therefore, be recommended under relatively saline conditions, while US 16-13-23 should be avoided.

Although the physiological response of the different rootstocks reflects differences in root density and root distribution (Southey, 1992), this does not preclude possible effects of differential ion uptake. This aspect is currently being investigated.

LITERATURE CITED

ALEXANDER, D. McE. & WOODHAM, R.C., 1968. Relative tolerance of rooted cuttings of four *vinifera* varieties to sodium chloride. *Aust. J. Exp. Agric. Animal Husb.* **8,** 461-465.

ARBABZADEH, F. & DUTT, G., 1987. Salt tolerance of grape rootstocks under greenhouse conditions. *Am. J. Enol. Vitic.* **38,** 95-99.

ARCHER, E. & STRAUSS, H.C., 1990. Effect of vine spacing on some physiological aspects of *Vitis vinifera* L. (cv. Pinot noir). *S. Afr. J. Enol. Vitic.* **11,** 76-86.

BARLASS, M. & SKENE, K.G.M., 1981. Relative NaCl tolerances of grapevine cultivars and hybrids *in vitro*. *Z. Pflanzenphysiol.* **102,** 147-156.

BERNSTEIN, L., 1975. Effects of salinity and sodicity on plant growth. *Ann. Rev. Phytopath.* **13,** 295-312.

DOWNTON, W.J.S., 1977. Photosynthesis in salt-stressed grapevines. *Aust. J. Plant Physiol.* **4,** 183-192.

DOWNTON, W.J.S., 1985. Growth and mineral composition of the Sultana grapevine as influenced by salinity and rootstock. *Aust. J. agric. Res.* **36,** 425-434.

DOWNTON, W.J.S., GRANT, W.J.R. & LOVEYS, B.R., 1987. Diurnal changes in the photosynthesis of field-grown grapevines. *New. Phytol.* **105,** 71-80.

DOWNTON, W.J.S. & MILLHOUSE, J., 1985. Chlorophyll fluorescence and water-relations of salt-stressed plants. *Plant. Sci. Lett.* **37,** 205-212.

DURING, H. & LOVEYS, B.R., 1982. Diurnal changes in water relations and abscisic acid in field-grown *Vitis vinifera* cvs. I. Leaf water potential components and leaf conductance under humid temperate and semi-arid conditions. *Vitis* **21,** 223-232.

GALE, J., 1975. Water balance and gas exchange of plants under saline conditions. In: POLJAKOFF-MAYBER, A. & GALE, J. (eds.). Plants in saline environments. Springer Verlag, New York, USA. pp. 168-185.

GREENWAY, H. & MUNNS, R., 1980. Mechanisms of salt tolerance in non-halophytes. *Ann. Rev. Plant Physiol.* **31,** 149-190.

GROOT OBBINK, J. & ALEXANDER, D. McE., 1973. Response of six grapevine cultivars to a range of chloride concentrations. *Am. J. Enol. Vitic.* **24,** 65-68.

HOFÄCKER, W., 1978. Investigations on the photosynthesis of vines. Influence of defoliation, topping, girdling and removal of grapes. *Vitis* **17,** 10-22.

HUNTER, J.J. & VISSER, J.H., 1988. The effect of partial defoliation, leaf position and developmental stage of the vine on photosynthetic activity of *Vitis vinifera* L. cv. Cabernet Sauvignon. *S. Afr. J. Enol. Vitic.* **9,** 9-15.

KRIEDEMANN, P.E., 1977. Vineleaf photosynthesis. In Proc. Int. Symp. on the Quality of the Vintage, 14-21 Feb, Cape Town. pp. 67-87.

LIU, W.T., POOL, R., WENKERT, W. & KRIEDEMANN, P.E., 1978. Changes in photosynthesis, stomatal resistance and abscisic acid of *Vitis labruscana* through drought and irrigation cycles. *Am. J. Enol. Vitic.* **29,** 239-246.

NAGARAJAH, S., 1989. Physiological responses of grapevines to water stress. *Acta. Hort.* **290,** 249-256.

RICHARDS, L.A. & U.S. SALINITY LABORATORY STAFF., 1954. Diagnosis and improvement of saline and alkaline soils. USDA Handbook no. 60. U.S. Govt. Printing Office, Washington D.C., USA.

SALISBURY, F.B. & ROSS, C.W., 1978. Plant physiology. Wadsworth Publishing Company, Inc., Belmont, California, USA.

SAUER, M.R., 1968. Effects of vine rootstock on chloride concentration in Sultana scions. *Vitis* **7,** 223-226.

SCHOLANDER, P.F., HAMMEL, H.T., BRADSTREET, E.D. & HEMMINGSON, E.A., 1965. Sap pressure in vascular plants. *Science* **148,** 339-346.

SEPULVEDA, G. & KLIEWER, W.M., 1986. Stomatal response of three grapevine cultivars (*Vitis vinifera* L.) to high temperature. *Am. J. Enol. Vitic.* **37,** 44-52.

SMART, R.E., 1974. Photosynthesis by grapevine canopies. *J. Appl. Ecol.* **11,** 997-1006.

SMART, R.E. & COOMBE, B.G., 1983. Water relations of grapevines. In: KOZLOWSKI, T.T. (ed.). Water deficits and plant growth. Academic Press, New York, USA. pp. 137-196.

SOUTHEY, J.M., 1992. Root distribution of different grapevine rootstocks on a relatively saline soil. *S. Afr. J. Enol. Vitic.* **13,** 1-9.

SOUTHEY, J.M. & JOOSTE, J.H., 1991. The effect of grapevine rootstock on the performance of *Vitis vinifera* L. (cv. Colombard) on a relatively saline soil. *S. Afr. J. Enol. Vitic.* **12,** 32-41.

VAN ZYL, J.L., 1984. Interrelationships among soil water regime, irrigation and water stress in the grapevine (*Vitis vinifera* L.) Ph.D. dissertation, University of Stellenbosch, 7600 Stellenbosch, Republic of South Africa.

WEST, D.W. & TAYLOR, J.A., 1984. Response of six grape cultivars to the combined effects of high salinity and rootzone waterlogging. *J. Amer. Soc. Hort. Sci.* **109,** 844-851.

WALKER, R.R., TÖRÖKFALVY, E., SCOTT, N.S. & KRIEDEMANN, P.E., 1981. An analysis of photosynthetic response to salt treatment in *Vitis vinifera*. *Austr. J. Plant Physiol.* **8,** 359-374.